An overview of the Hookeriales

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The Hookeriales have been considered to be one of the more homogeneous orders of mosses. Suborders Ephemeropsidineae (= Nematacineae) and Hookeriineae have been distinguished for many years on the basis of the gametophyte being reduced to a protonema bearing sexual buds in the first and a normal leafy gametophyte in the second. The common bond within the order is based almost entirely on the usually small, often roughened, sporophyte with a double peristome, the conical to mitriform, often fringed, calyptra, a comparatively lax areolation and an absence of alar cells. The "hookeriaceous" peristome is usually characterized by a lamellate exostome somewhat taller than the endostome with its low to medium basal membrane and simple processes which are only rarely separated by a single cilium. As Crosby (1969) correctly observed of the Hookeriaceae as defined by Brotherus (1925), "one finds no character or group of characters that unite the group." However, one can find an aggregate of features among groups of genera which can be aligned to show a common heritage even though not all are present in any single genus or group of allied genera. Welch (1966, 1969) has considered the Hookeriaceae in the broad sense.

The acknowledged heterogeneity of the Hookeriaceae as defined by Brotherus can be better understood if we recognize that his description and arrangement is essentially an abridgement of Fleischer's system presented in 1908. The success of Fleischer's system for the mosses is due to his acceptance of the concepts of evolution, as known at that time, and their application to develop an arrangement on something other than an artificial basis. Bessey's "dicta" presented in 1915 indicating the importance of reduction as one aspect of evolutionary advancement had not yet appeared in a refined form, so we find that, for the most part, the taxa have been placed in a simple to complex order. Further,

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great stress was placed on the structure of the peristome and the morphology of the gametophyte was considered to be of somewhat lesser importance. If both sporophytic and gametophytic structures are taken into account, and if we allow reduction as an indication of advancement, the Hookeriaceae can be rearranged into several comparatively homogeneous groups with a common heritage.

Because the reorganization proposed differs considerably in some ways from the Fleischer-Brotherus system, my principles of classification are listed below. In utilizing the principles the following general premises, derived in the main from Hutchinson (1959), must be taken into account: 1) evolution is both upwards and downwards, the latter involving degradation and degeneration; 2) evolution does not involve all organs, or both generations, at the same time and both elaboration and degeneration may be occurring at the same time; and 3) evolution has generally been consistent with a particular tendency potentially being carried to the extreme of elaboration or reduction although the extremes may not be present in extant groups.

Some Principles for Moss Systematics

N.B. The principles are arranged from general to specific features, but no relative importance is to be implied from the order.

1. Within any group, the larger mosses are generally more primitive than smaller ones.

2. Closely attached forms with all stems leafy are more primitive than stoloniferous forms.

3. Perennial mosses are more primitive than the annual or ephemeral species including those with a persistent protonema.

4. Both completely aquatic and xerophytic forms are derived from an aerial, but almost constantly moist, ancestor.

5. A central strand in the stem is a primitive feature.

6. Stems with a several-layered cortex comprised of thick-walled or stereid cells are more primitive than stems with a unistratose or undifferentiated cortex.

7. Leaf gaps are a primitive feature.

8. Radial leaf arrangement is more primitive than distichous arrangement with the complanate condition probably intermediate.

9. A strong costa is more primitive than a weak one with the ecostate condition most derived.

10. An excurrent costa is an advanced characteristic sometimes associated with blade reduction.

11. Well developed alar cells may be an advanced condition.

12. Smooth leaf cells may be primitive with papillate cells the derived condition.

13. Extremely thin-walled or thick-walled cells are derived.

14. Specialized vegetative reproduction by brood-bodies is more advanced than vegetative propagation by simple fragmentation and regeneration.

15. Monoicous sexuality is more primitive than the dioicous condition.

16. Numerous gametangia and paraphyses are more primitive than few archegonia or antheridia per inflorescence.

17. Sexual dimorphism, expressed in the extreme by the formation of dwarf males and the heterosporous tendency, as in some species of Macromitrium and Homalothecium, is advanced.

18. An elongate seta bearing an exposed capsule is more primitive than a short seta with an immersed capsule.

19. A capsule wall with stomata, especially when associated with air chambers, represents a more primitive condition than the capsule lacking stomata.

20. Cleistocarpy is probably a derived condition in the Bryidae.

21. A reduced endostome lacking processes on the basal membrane is advanced over one with processes and a high basal membrane; the presence of cilia may also be advanced.

22. A peristome which is very much reduced or absent is derived from a normal peristome.

23. Retention of the operculum or a portion of it on the columella is an advanced condition.

Several taxonomically useful morphological variants are not included above because I have been unable to divine the relative conditions of such things as leaf borders, lamellae, cell shapes, paraphyllia, plane vs. keeled structures, single vs. double peristomes, acrocarpy vs. pleurocarpy (there is good evidence both ways), calyptra type, and a multitude of structural features of the peristome such as median lines, surface, striations, and accessory ornamentation. Surely the list may be substantially revised, but if it serves to stimulate development of a better classification and critical morphological research, the purpose will have been well served.

As defined until Crosby's (1969) Pilotrichum revision appeared, the Hookeriineae was comprised of the Pilotrichaceae, Hookeriaceae, and the Hypopterygiaceae. Because he found little difference between Pilotrichum and Helicoblepharum or among Thamniopsis, Pilotrichidium and Diploneuron, Crosby merged the Pilotrichaceae with the Hookeriaceae. He apparently was correct in his evaluation of the generic relationships of Pilotrichum with members of the Hookeriaceae as defined at that time. If we consider the position of Pilotrichum and its allied species within the order, it is among the more primitive types and quite distinct from all but a few genera customarily included in the Hookeriaceae-Hypnelloideae. In such a case it seems best to set this group apart as the family Pilotrichaceae and to arrange the genera within it in as natural a sequence as possible.

From some Pilotrichaceous type, one may derive the Hookeriaceae-Hookeriopsidoideae with a long double costa, elongate seta, complanate foliage, and a pinnate habit. This, in turn, mainly by reduction of the costa and seta along with

the development of comparatively lax areolation, leads to the Hookeriaceae-Hookerioideae.

The Hookerioideae, perhaps through a common ancestor to Eriopus, link to the Distichophyllaceae characterized by the asymmetric, bordered, once costate, parenchymatous more or less isodiametrically areolate leaves and the cross-striate peristome. Müller suggested that this group be recognized as the family Mniadelphaceae nearly 100 years ago but no description was included so his name cannot stand.

The Daltoniaceae resemble the Distichophyllaceae in the bordered leaves with a single costa and isodiametric cells but differ in their smaller size, radial symmetry, uniform leaves, upright habit and their selection of ephemeral habitats as twigs, leaves, and even the backs of large weevils in the cloud forests of New Guinea. The peristome differs from others in the order in that both ranks are strongly papillose and well-developed with the exostome lacking striae.

It is quite likely that Daltonia and Ephemeropsis have a common origin but the separation, as evidenced by the striate rather than papillose peristome, is great and doubtless of long standing. Fossils of Ephemeropsis have been found in middle Eocene deposits from Germany suggesting that it was once more widely distributed than just to Malesia and New Zealand as at present. Continued recognition of the family in a separate suborder seems quite proper.

Although Fleischer and Brotherus placed the Symphyodontaceae and Leucomiaceae in the Hookeriales, Dixon (1932) assigned them to the Hypnales (assuming that "Symphysodontaceae" is a mis-print or lapsus for Symphyodontaceae). The morphology of the gametophyte is suggestive of Vesicularia and allied Hypnaceous genera but the evidence is not clear. Unfortunately, Dixon did not give any explanation for the shift which has not been taken up by Bartram (1939, 1949), Crum and Bartram (1958), or Crum and Steere (1957), for example. The leaves of Symphyodon have a few alar cells but the erect, spiny, purple, capsule with simple papillose exostome teeth and a reduced endostome is quite unlike that characteristic of the Hypnaceae. Leucomium has a Hookeria-like peristome and shares the very large thin-walled cells characteristic of Hookeria as well. Until some evidence can be offered to substantiate Dixon's opinion, I am satisfied that these families can be reasonably considered among the Hookeriales.

A specialized derivative, probably from the Distichophyllaceae, is the Hypopterygiineae comprised of the Hypopterygiaceae and the Cyathophoraceae. The complanate habit is carried to the extreme with the development of markedly different obliquely inserted, wide-spreading, lateral leaves and reduced, transverse, erect, amphigastrial leaves. A stipe with widely spaced, often scale-like, leaves or a prostrate stoloniferous stem is developed. The very short to absent costa, regular alignment of the amphigastria, and very short seta serve to set off the Cyathophoraceae from the Hypopterygiaceae.

In the following revision I have arranged the taxa so far as possible according to the principles listed above. As the positions of the genera are subject to various interpretations depending upon the importance placed on one feature or another, I have not attempted to further justify the sequence of genera as presented. Some groups remain heterogenous and may be defined ultimately in somewhat different ways.

ORDER HOOKERIALES

Suborder Hookeriineae

Pilotrichaceae

1. Hemiragis
2. Thamniopsis
3. Stenodictyon
4. Pilotrichidium
5. Diploneuron
6. Callicostellopsis
7. Helicoblepharum
8. Pilotrichum
9. Hypnella
10. Neohypnella
11. Acrohypnella
12. Chaetomitriopsis
13. Chaetomitrium
14. Orontobryum
15. Dimorphocladon

Hookeriaceae

Hookeriopsidoideae, subfam. nov. Folium cum costa duplici ad vel supra medium folium soluta; cellulae laeves vel unipapillatae. Exostomium cum dentibus hyalinis et papillosis aut rubris vel brunneolis et cruciatistriatis; endostomium plerumque flavidum, cum membrana basali processus subulatos papillosos carinatos ferens. Typus: Hookeriopsis (Besch.) Jaeg.

Leaves with a double costa usually extending to mid-leaf or beyond, narrowly bordered to unbordered; cells smooth to unipapillate over the lumen. Peristome double; exostome pale to hyaline and papillose or red to brown and cross-striate; endostome pale yellow to brownish, basal membrane bearing keeled papillose processes with no, or rarely rudimentary, intercalated cilia.

1. Amblytropis
2. Cyclodictyon
3. Archboldiella
4. Lepidopilidium
5. Actinodontium
6. Lepidopilum
7. Hookeriopsis
8. Callicostella

Hookérioideae

1. Hookeria
2. Tetrastichium
3. Schimperobryum (= Lamprophyllum)
4. Crossomitrium
5. Eriopus

Distichophyllaceae, fam. nov.

Caulis diversifolius; foliis plerumque asymmetricis et limbatis; costa singulari, infra apicem soluta sed interdum percurrens; cellulae hexagonae vel rhombiformes cum parietibus tenuibus et laevibus, aut rotundae cum parietibus incrassatis et interdum papillosis. Typus: Distichophyllum Dozy et Molkenb.

Leaves of varying size and shape on the same stem, usually asymmetrical and generally bordered; costa single usually ending below the apex but sometimes percurrent; cells generally thin-walled and hexagonal above, but sometimes rhombid, or thick-walled and ronded, smooth or (in Adelothecium) papillate over the lumen. Peristome double with the exostome well developed and the endostome with a high basal membrane and long processes or a low membrane and reduced teeth or absent.

1. Pterygophyllum
2. Distichophyllum
3. Distichophyllidium
4. Leskeodon
5. Leskeodontopsis
6. ? Adelothecium

The position of Adelothecium in this family is questionable although the peristome is very similar to the others and the leaves have a single costa. It differs in the leaves being unbordered with incrassate, strongly truncate-papillate cells. If another alliance cannot be found for the genus it should probably be placed in a separate subfamily.

Daltoniaceae, fam. nov.

Plantae gregariae vel caespitosae, plerumque parvae, epiphyticae, leviter nitidae, dilute virides vel aureae sunt. Folia aequabiles, erectiuscula vel erecto-patentia; margine limbato et integro; costa singula et infra apice soluta; cellulis rhombis vel rotundis, laevibus. Peristomium duplex, exterius et interius pariter longus. Typus: Daltonia Hook. & Tayl.

Gregarious to turf-forming, usually small and little branched, epiphytic, faintly shiny plants. Leaves uniform, symmetrical, and erect-spreading; margin bordered and mostly entire; costa single, ending below or in the apex; cells rhomboid to rounded and smooth. Peristome double with the exostome the same length as the endostome and papillose (except Bellia); endostome usually with a low basal membrane bearing keeled, subulate, papillose processes.

1. Bellia
2. Daltonia

Symphyodontaceae

1. Symphyodon

Leucomiaceae

1. Vesiculariopsis
2. Philophyllum
3. Sauloma
4. Leucomium
5. Pulvinella
6. Stenodesmus
7. Rhynchostegiopsis

Suborder Ephemeropsidineae (Nematacineae)

Ephemeropsidaceae (Nemataceae)

1. Ephemeropsis (including Archephemeropsis)

Suborder Hypopterygiineae, subord. nov.

Rami cum foliis in stipite ex caule rhizomate errigens. Folia dimorpha, amphigastriis comparate parvis et transverse affixis autem foliis lateralibus oblique insertis. Typus: Hypopterygiaceae.

Leafy branches stipitate from a rhizome-like stem and usually dendroid or pinnately branched; central strand strong. Leaves of two types; lateral leaves obliquely to nearly longitudinally inserted, usually plane and oblong; ventral leaves transverse or nearly so, erect, often lanceolate to subulate, and smaller than lateral leaves, being true amphigastria. Peristome double or the exostome lacking; endostome with a plicate basal membrane and keeled processes.

Hypopterygiaceae

1. Lopidium
2. Hypopterygium
3. Catharomnium

Cyathophoraceae, fam. nov.

Plantae gregariae, arboricolae aut in saxo humido, cum caulibus foliosis simplicibus et stipitibus brevibus. Folia dimorpha, amphigastriis imbricatis et in specie singulari, foliis lateralibus distichis; cellulis tenuiparietibus, hexagonis. Fructus in axillis amphigastriorum; seta brevi; capsula globosa vel cylindrica; peristomium duplex, exterius cum dentibus 16 lanceolatis et interius cum dentibus 16 lanceolatis in membrana basali alta; operculum conicum rostratum. Calyptra conica et parva.

Usually large, gregarious plants rising from a brown, densely tomentose rhizome attached to moist, shaded, tree trunks, logs, or damp rocks, with the simple leafy branches usually horizontal and stipitate below. Leaves dimorphic, the imbricate amphigastria in a single row, lateral leaves distant, obliquely inserted on either side of the stem and somewhat asymmetric; cells thin-walled, isodiametric to elongate-hexagonal, smooth, and punctulate. Dioicous with sexual buds in axils of the amphigastria. Seta short, smooth, with an erect, globose to cylindrical, thick-necked capsule; annulus broad; peristome double; exostome with 16 lanceolate teeth; endostome with a high basal membrane bearing lanceolate processes; operculum conic and beaked. Calyptra conic and small.

1. Cyathophorum
2. Cyathophorella

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